The Veliger 29(4):359-366 (April 1, 1987)

THE VELIGER

Morphological Classification of Sibling Species of *Littorina* (Gastropoda: Prosobranchia): Discretionary Use of Discriminant Analysis

by

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Abstract. The sibling species *Littorina plena* and *L. scutulata* show considerable intraspecific variation in shell morphology, with wide overlap in shell characters between species. Measures of single characters (length-to-width ratio, apical angle, number of whorls, degree of tessellation, and presence of one spiral amber band in the shell aperture) are not sufficient for accurate separation and classification of specimens. However, discriminant functions that use statistically derived combinations of several easily measured shell characters allow approximately 92% of the snails from the exposed coast near Bodega Bay, California, to be correctly classified, and significantly improve morphological discrimination of these sibling species.

The shell morphology of *Littorina scutulata* and *L. plena* varies geographically and between habitats. Variability in morphological characters may be as great within a species as between species when individuals are considered from several sites. Only 47% of individual *L. plena* are correctly classified when the discriminant functions derived for open coast populations are applied to snails from nearby protected habitats. Although discriminant analysis is a powerful technique for distinguishing between morphologically similar species, such variation in morphology emphasizes the need to derive and evaluate discriminant functions for specific populations.

INTRODUCTION

TAXONOMIC STATUS has been the subject of study for several species of marine littoral gastropods in the genus *Littorina*. Intraspecific variation in shell characters and wide overlap between species have at times made morphological identification of species complicated and ambiguous, and taxonomists have had to rely upon other sources of information to detect or confirm the presence of sibling (morphologically similar) species of *Littorina*. Differences in mode of reproduction (HELLER, 1975a), morphology of genitalia (WHIPPLE, 1965; HELLER, 1975a; GOODWIN & FISH, 1977), characteristics of spawn (WHIPPLE, 1965; BORKOWSKI & BORKOWSKI, 1969), and allele frequencies at certain gene-enzyme loci (HELLER, 1975a; WARD & WARWICK, 1980; WILKENS & O'REGAN, 1980; MASTRO *et al.*, 1982) have been used to establish the existence of separate species in cases where morphological data on shell characters alone were insufficient.

Within populations, many *Littorina* species exhibit considerable variation in shell size, shape, sculpture, color, and color pattern (for examples: BORKOWSKI, 1975; RAFFAELLI, 1979). Further morphological variation within a species can be attributed to environmental gradients in temperature (HUGHES, 1979), substratum (HELLER, 1975b), and exposure to wave action (STRUHSAKER, 1968; NEWKIRK & DOYLE, 1975; HYLLEBERG & CHRISTENSEN, 1977). Distinguishing between sympatric sibling species on the basis of shell morphology alone is tenuous when such intraspecific variability is present.

Where sympatric sibling species do occur, morphological classification of individuals is improved by removing interhabitat variation in shell characters. Separate diagnostic characters can be selected for each habitat in which the species coexist. If necessary, statistically derived combinations of shell characters can be employed to discriminate between sibling species in the same habitat.

Littorina plena Gould, 1849, and *Littorina scutulata* Gould, 1849, occur in sympatry along the west coast of North America. They are abundant microalgal grazers on

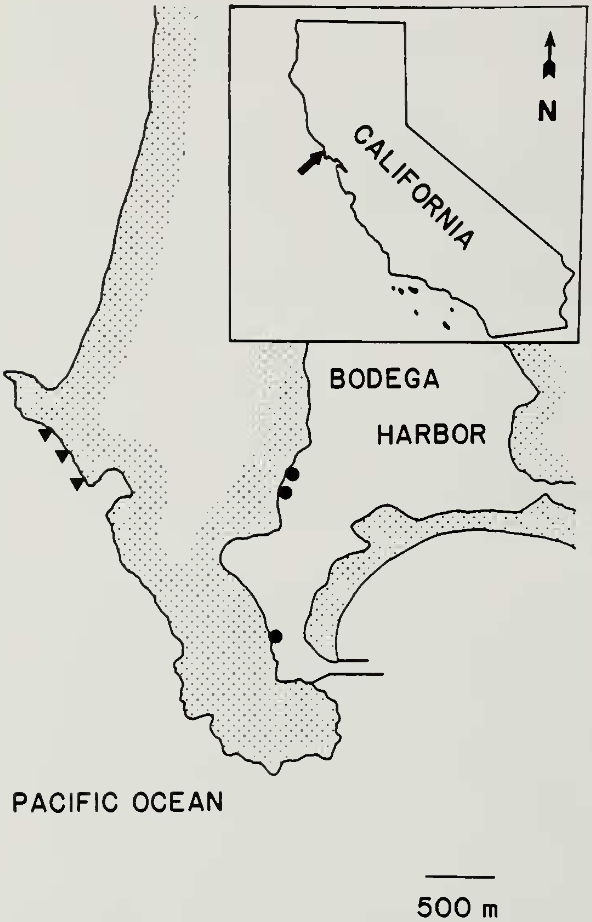

Figure 1

Location of study area on the biological reserve of the University of California Bodega Marine Laboratory: triangles indicate open coast sites and circles indicate protected harbor sites from which *Littorina* specimens were collected.

rocks and pilings in sheltered bays as well as on rocky shores of the exposed open coast. Reproductive distinctions detailed by MURRAY (1979) and patterns of genetic differentiation described by MASTRO *et al.* (1982) have verified the taxonomic status of *L. scutulata* and *L. plena* as separate sibling species. Both species, however, possess variable shell characteristics, and consistent differences in shell morphology have yet to be defined completely for these snails.

MURRAY (1982) uses the statistical techniques of discriminant analysis for morphological classification of *Littorina plena* and *L. scutulata* from a few locations along the west coast of the United States. However, satisfactory species characterization of the morphology of *Littorina* is likely to require control of local environmental (habitat) variables. This study describes in detail the morphology of snails from several populations near Bodega Bay, California, using techniques similar to those of MURRAY (1982), and emphasizes the potential hazards of using discriminant functions for organisms that show widespread geographical and habitat variation in morphology.

MATERIALS AND METHODS

Exposed Coast Populations of *Littorina*

Specimens of *Littorina plena* and *L. scutulata* were collected from exposed rocky shores northwest of Horseshoe Cove on the biological reserve of the University of California, Bodega Bay, California (Figure 1). Individuals were separated by species and sex according to the characters described by MURRAY (1979) and MASTRO *et al.* (1982). Male snails were identified by penis morphology and female snails by the type of egg capsule produced while isolated in individual containers. Only identifiable snails (spawning females and males with shell lengths greater than 4 mm) were used in this study of shell morphology.

Statistical analyses of morphological data were conducted on several shell characters, which included shell length, shell width perpendicular to the long axis, apical angle, number of whorls, degree of tessellated color pattern, and presence of one amber spiral band in the aperture. These characters were chosen for their ease of determination and for their initial promise in distinguishing *Littorina plena* from *L. scutulata.* Linear dimensions were measured to the nearest 0.01 mm with dial calipers held under a dissecting microscope and the apical angle was determined to the nearest degree with a protractor. The degree of tessellation and the appearance of the amber band were scored as either (0) absent, (1) obscure, or (2) distinct. All measurements were made on live animals with the aperture oriented upwards (Figure 2).

Discriminant Analyses for Exposed Coast Populations

An optimal set of shell characters for classifying exposed coast specimens of *Littorina plena* and *L. scutulata* was obtained by discriminant analysis. Discriminant analysis is a procedure that weights and linearly combines characteristics for which groups are expected to differ; the result is a discriminant function that maximizes statistical separation of the groups. It is then possible to identify those characteristics that contribute most to differentiation between the groups, and to derive functions that classify cases of unknown membership.

Discriminant analyses were performed on several subsets of the data, using a stepwise method of entering and removing shell characters as discriminating variables. The computer program for discriminant analysis obtained from the Statistical Package for Social Sciences (NIE *et al.*, 1975) began by selecting that character that best distinguished *Littorina plena* from *L. scutulata.* A second character was then selected as the variable best able to improve the power of discrimination when combined with the first char-

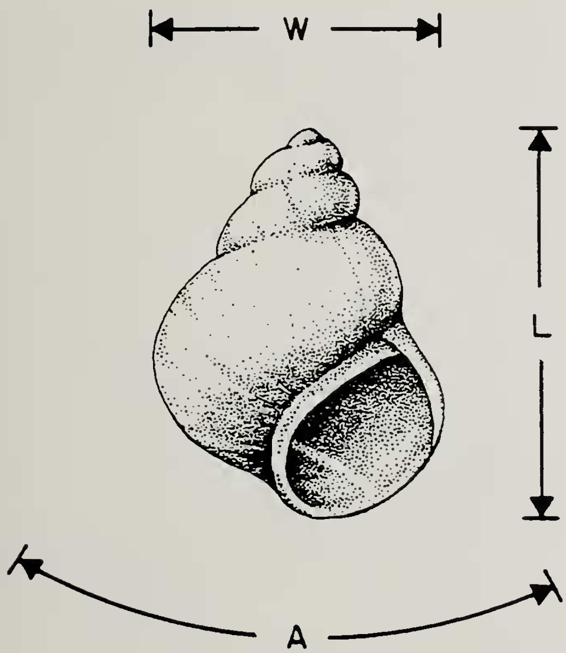

Figure 2

Morphological measurements made on each shell. L = shell length; W = shell width; A = apical angle. (Shell shown with amber band present inside the aperture.)

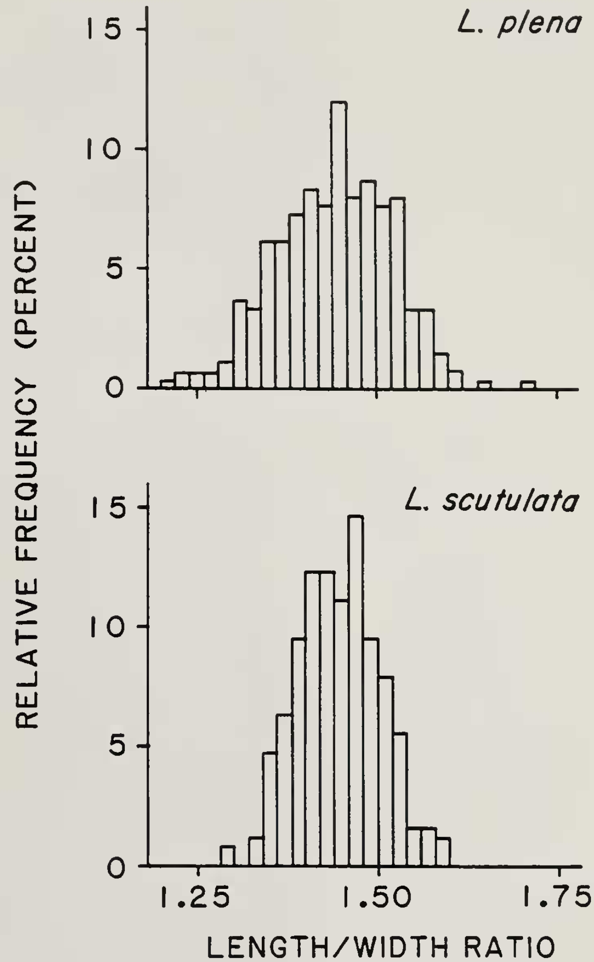

Figure 3

Frequency histograms of length-to-width ratios for *Littorina plena* (n = 275) and *L. scutulata* (n = 253). Distributions for the two species are not statistically different. Kolmogorov-Smirnov two-sample test: DMAX = 0.1001; $P > 0.10$.

acter. The third and subsequent characters were selected similarly in order of their explanatory power until all characters were selected. At each step, characters could be removed if they acted to reduce discrimination in combination with more recently selected characters. Standardized (weighting) coefficients were eventually produced that indicated the relative importance of each of the characters finally chosen. COOLEY & LOHNES (1971) and TATSUOKA (1971) have described the mathematical techniques involved.

Snails from exposed coast populations were used to derive discriminant functions for *Littorina plena* and *L. scutulata.* From samples collected monthly during the period September 1980 to December 1981, a subsample of 275 *L. plena* and 253 *L. scutulata* was selected randomly for discriminant analyses. Smaller sample sizes were used for some analyses, and individuals selected were restricted to shell lengths less than 13 mm because all snails larger than 13 mm were *L. scutulata.*

Suitability of Derived Discriminant Functions

Specimens were collected between May 1984 and October 1984 from the exposed coast study site and from additional sites inside a protected harbor located 1.5–2.0 km from the exposed coast site (Figure 1). These samples were used to test the general applicability of the previously derived discriminant functions. Thirty-four *Littorina plena* and 33 *L. scutulata* were obtained from the exposed coast habitat to examine the usefulness of the discriminant functions over long periods of time. The capacity of the discriminant functions to classify individuals from a different habitat was measured on a sample of 57 *L. plena* and 22 *L. scutulata* obtained from the protected harbor habitats. Harbor snails were identified and measured using the same methods as described for exposed coast snails.

RESULTS

Exposed Coast Populations of *Littorina*

Littorina plena and *L. scutulata* from the exposed coast exhibited considerable overlap in all shell characters examined in this investigation. Frequency histograms of length-to-width ratios (Figure 3) failed to reveal any sta-

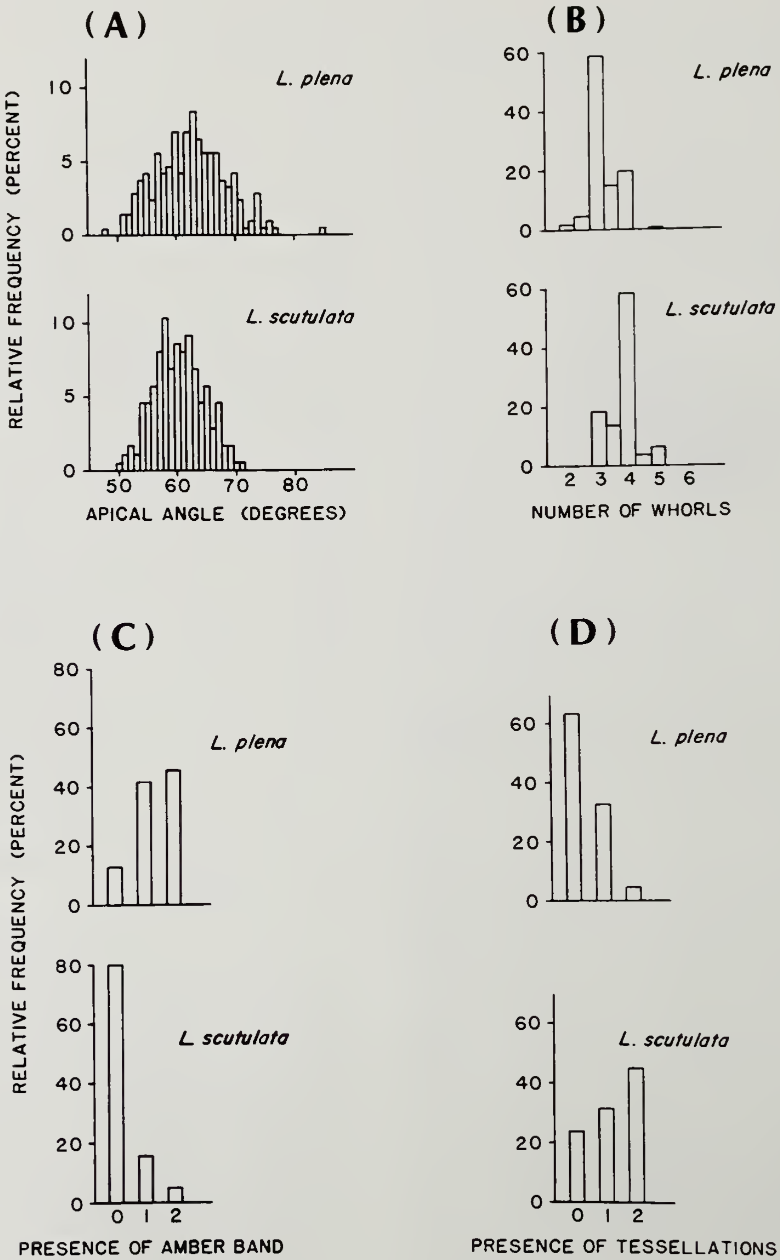

Figure 4

Frequency histograms of shell characters for *Littorina plena* and *L. scutulata*. n_p = sample size for *L. plena*; n_s = sample size for *L. scutulata*. Species differences in all shell characters are significantly different (Kolmogorov-Smirnov two-sample tests; all $P < 0.01$). A, apical angles ($n_p = 216$; $n_s = 174$; DMAX = 0.2208); B, number of whorls ($n_p = 333$; $n_s = 315$; DMAX = 0.4783); C, occurrence of amber band in the aperture (0 = absent; 1 = obscure; 2 = distinct) ($n_p = 280$; $n_s = 272$; DMAX = 0.6692); D, occurrence of tessellated color patterns on shell (0 = absent, 1 = obscure; 2 = distinct) ($n_p = 92$; $n_s = 122$; DMAX = 0.4073).

tistical differences in general shell shape between these two sibling species. However, specimens of *L. scutulata* attained a larger size than those of *L. plena* (snails with shell lengths greater than 13 mm were invariably *L. scutulata*). Moreover, shells from these populations of *L. plena* and *L. scutulata* displayed statistically significant differences in the apical angle, number of whorls, degree of tessellation, and presence of an amber band in the aperture (Figure 4).

Individual *Littorina plena* generally had larger apical

angles, and the population as a whole showed greater variation ($F = 1.95$; d.f. = 215, 173; $P < 0.01$), than *L. scutulata*. The average apical angle (mean ± SD) for *L. plena* was 62.6 ± 6.0 while apical angles averaged 60.2 ± 4.3 for *L. scutulata*. Figure 4A presents sample sizes and distributions of apical angles for each of the sibling species.

Shells of *Littorina plena* usually had fewer whorls than those of *L. scutulata* (Figure 4B). Only 20% of the *L. plena* specimens examined ($n = 335$) had four or more whorls, while 68% of the *L. scutulata* shells ($n = 315$) had at least four whorls.

Littorina plena shells were more likely to possess an amber band in the aperture (Figure 4C), but less likely to show tessellations (Figure 4D) than those of *L. scutulata*. In 87% of the *L. plena* specimens ($n = 280$) the band was present to some extent; the band was observed in only 20% of the *L. scutulata* shells ($n = 272$). Thirty-seven percent of the *L. plena* shells inspected ($n = 92$) displayed at least some degree of tessellation; in contrast, a tessellated pattern was present on 76% of the *L. scutulata* shells ($n = 122$), and this pattern was more often very prominent than on *L. plena* shells.

Discriminant Analyses for Exposed Coast Populations

Although the differences between *Littorina plena* and *L. scutulata* in some shell characters were statistically significant, no one character accurately separated individuals to species. Reliability of identification was enhanced by simultaneously using several characters through discriminant analysis. Table 1 lists discriminant functions for three analyses using the following subsets of shell characters: (1) length, width, presence of amber band, and number of whorls; (2) length, width, presence of amber band, number of whorls, and presence of tessellations; and (3) length, width, presence of amber band, number of whorls, and apical angle. A discriminant score was computed for each individual by multiplying each of the snail's shell characters by the corresponding coefficient and adding together these products. The resulting discriminant score represented the number of standard deviations that snail was away from the mean of all snails (both species)

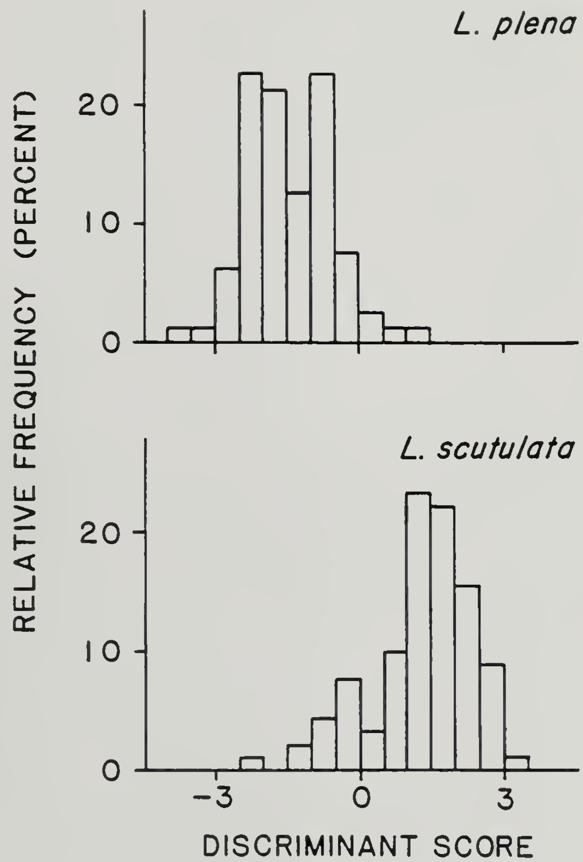

Figure 5

Frequency histograms of discriminant scores for *Littorina plena* ($n = 80$) and *L. scutulata* ($n = 90$). Discriminant score = $-0.882L + 1.662W - 1.274B + 0.821WH + 0.473T - 4.644$ where: L = shell length in mm; W = shell width in mm; B = presence of amber band in aperture; WH = number of whorls; T = extent of tessellated color pattern. B and T are scored (0) absent, (1) obscure, or (2) distinct. Distributions are significantly different. Kolmogorov-Smirnov two-sample test: DMAX = 0.7972; $P \ll 0.01$.

Table 1

Discriminant functions for three sets of shell characters: L = shell length in mm; W = shell width in mm; B = presence of amber band in aperture, scored 0–2; WH = number of whorls; T = extent of tessellated color pattern scored 0–2; A = apical angle in degrees. Sample sizes (n) indicate the numbers of each species from open coast populations used in the analysis. Mean discriminant scores indicate the species' means for each function. SD = standard deviation.

Analysis	Function	*Littorina plena* n	*Littorina plena* Mean	*Littorina plena* SD	*Littorina scutulata* n	*Littorina scutulata* Mean	*Littorina scutulata* SD
1	$D = -0.732L + 1.599W - 0.983B + 1.306WH - 6.952$	256	−1.128	0.940	215	1.343	1.067
2	$D = -0.882L + 1.662W - 1.274B + 0.821WH + 0.473T - 4.644$	80	−1.459	0.920	90	1.297	1.066
3	$D = -1.369L + 2.514W - 0.812B + 1.514WH - 0.064A - 3.798$	156	−1.119	0.923	125	1.396	1.089

Table 2

Standardized discriminant function coefficients for each analysis of *Littorina plena* and *L. scutulata*. See text for explanation.

Analysis	Coefficients for each shell character: Shell length	Shell width	Amber band	Whorls	Tessellations	Apical angle
1	−1.003	1.409	−0615	0.629	—	—
2	−1.036	1.299	−0.704	0.398	0.331	—
3	−1.991	2.338	−0.530	0.702	—	−0.351

on the given discriminant function. Table 1 indicates the number of snails used in the analyses and the mean discriminant scores for *L. plena* and *L. scutulata* for each of the discriminant functions. The extent to which the two species were separated by discriminant analysis is shown in Figure 5 (for the function that utilized shell length, width, presence of amber band, number of whorls, and degree of tessellation as discriminating variables).

Standardized (weighting) coefficients for each discriminant function are given in Table 2. The absolute value of a coefficient indicates the relative contribution of the associated shell character to that particular function. (The sign of the coefficient simply denotes whether the character is making a positive or negative contribution.) In all three analyses, shell width and shell length had the greatest importance in separating *Littorina plena* from *L. scutulata*. Apical angle and degree of tessellation were least important.

Individuals were assigned to species through the use of classification functions. Classification functions are usually employed to classify new individuals with unknown identities, but were used in this analysis to test the adequacy of the discriminant functions. As with the discriminant functions, classification scores were obtained by multiplying character values by the appropriate coefficients and summing these products. For each analysis, there was a separate equation for each species; the resulting classification scores quantified the likelihood that an individual belonged to the corresponding species, and the individual was then assigned to the species for which it had the greatest likelihood of membership (the highest classification score). Classification functions and the percent of correct classifications (*i.e.,* those confirming the reproductive characters) are given in Table 3 for each species for the three statistical analyses. (Additional specimens from exposed coast populations, not included in the initial analyses, were added to the samples of snails classified.) The best classification of species was obtained when length, width, presence of an amber band, number of whorls, and presence of tessellations were employed as discriminating characters; better than 95% of the *L. plena* and 89% of the *L. scutulata* were correctly identified.

Suitability of Derived Discriminant Functions

Discriminant and classification functions derived for exposed coast populations of *Littorina plena* and *L. scutulata* (using length, width, presence of an amber band, number of whorls, and presence of tessellations as discriminating characters) correctly identified high proportions of snails collected from the same location three years later. The average discriminant score (mean ± SD) for *L. plena* collected at the later date was −1.492 ± 0.854 and 97% of the individuals ($n = 34$) were properly classified. The average discriminant score for *L. scutulata* was 0.845 ± 1.092 and 82% of the individuals ($n = 33$) were properly classified.

The same functions successfully classified 86% of the *Littorina scutulata* collected from protected harbor habitats (average discriminant score = 1.063 ± 0.872; $n = 22$). However, only 47% of the *L. plena* from protected harbor habitats were correctly classified (average discriminant score = −0.063 ± 0.971; $n = 57$). Individuals of both species tended to have more whorls and a higher degree of tessellation when collected from the harbor compared

Table 3

Classification functions for each discriminant analysis. Also shown are the percentages of correct identifications for each species and for each analysis. (Sample sizes are given in parentheses and include additional open coast snails to those used in the initial analysis.) C_p = classification score for *Littorina plena*; C_s = classification score for *L. scutulata*. Other abbreviations the same as for Table 1.

Analysis	Classification functions	Percent correctly identified: *L. plena*	*L. scutulata*	Total
1	$C_p = -11.76L + 24.63W + 5.07B + 18.13WH - 53.86$	89.82	88.14	89.02
	$C_s = -13.57L + 28.58W + 2.64B + 21.36WH - 71.31$	(275)	(253)	(528)
2	$C_p = -8.35L + 23.09W + 8.43B + 18.20WH - 0.33T - 67.71$	95.65	89.34	92.06
	$C_s = -10.78L + 27.67W + 4.92B + 20.46WH + 0.97T - 80.29$	(92)	(122)	(214)
3	$C_p = 38.40L - 49.21W + 5.49B + 9.00WH + 4.54A - 174.95$	92.64	85.50	89.46
	$C_s = 34.94L - 42.89W + 3.45B + 12.81WH + 4.38A - 184.84$	(163)	(131)	(294)

to snails found on the exposed coast. These morphological changes in the harbor habitat increased the likelihood that any particular snail would be classified as *L. scutulata* by discriminant analysis, and thus significantly increased the probability of mistakenly classifying harbor specimens of *L. plena* (adjusted chi-square = 43.87; d.f. = 1; $P < 0.001$).

DISCUSSION

For gastropods that show as much intraspecific variability in shell morphology as *Littorina* (Whipple, 1965; Borkowski, 1975; Raffaelli, 1979), morphological discrimination of sibling species becomes a difficult task. Morphological features of the shell are usually the most convenient, rapid, and inexpensive means for classifying individuals from different species, being applicable to living snails and dried shells alike. In the case of sibling species, however, specific diagnostic characters may be lacking. It may be necessary to rely upon statistical techniques that incorporate several shell characters in order accurately to identify species by morphology.

Adult *Littorina plena* and *L. scutulata* from the exposed coast near Bodega Bay differ significantly in several shell characters, supporting previous conclusions (Murray, 1979, 1982; Mastro *et al.*, 1982) that the two species are indeed separate taxonomic entities. Individual *L. scutulata* reach a larger size, and usually possess more whorls and tessellations than *L. plena*. Yet, classification of these individuals based on shell morphology alone requires measurements of many morphological variables and a statistical procedure for evaluating these variables. Using four or five variables, the discriminant analyses performed in this study correctly assign snails to species in approximately 90% of the cases. Discriminant scores further measure the reliability of identification on an individual by individual basis; greater confidence can be placed in individual identifications that have extreme discriminant scores.

However, the plasticity of shell morphology in single species of *Littorina* can result in distinct morphological alterations along environmental and geographic gradients (Colman, 1932; Struhsaker, 1968; Vermeij, 1973; Newkirk & Doyle, 1975; Hughes, 1979). In fact, the shells of both *L. plena* and *L. scutulata* from Bodega Bay reach larger sizes, possess more whorls and tessellations, and have taller spires as populations occupy more sheltered habitats. As a result, *L. plena* from sheltered habitats begin to look like *L. scutulata* from exposed habitats, while *L. scutulata* from sheltered habitats look like more extreme forms of *L. scutulata* from exposed habitats. Such variation in shell features with changes in habitat reduces the utility of the specific discriminant functions derived in this study. Clearly, systematic biases in classification occur when discriminant functions for exposed coast populations are applied without adjustment to individuals from nearby sheltered bays. Specimens of one species from one habitat overlap in morphology with specimens of the second species from a different habitat.

Taxonomic separation of species based on morphology usually assumes that differences between species are greater than differences within a species. Colman (1932) states that two morphs are not separate species unless it is shown, "after the examination of sufficient numbers collected over a wide area, that there is not a series of overlapping intergrades between the two differing forms." However, this stipulation for species status is conservative and makes no allowance for the existence of sibling species. Morphological overlap increases between the sibling species *Littorina plena* and *L. scutulata* when specimens are considered from a variety of habitats.

Morphological characterizations of sibling species of *Littorina* are likely to lack discriminating power if considered for the full geographic range of the species. Murray (1982) presents a discriminant analysis for *L. plena* and *L. scutulata* morphologies that is based on small samples combined from several sites along the western coast of the United States. Such an analysis may obscure important interhabitat shell variation if a wide variety of environments is considered, or may seriously bias the morphological descriptions if samples from particular habitats are unduly represented. Snails from the exposed rocky shores near Bodega Bay differ significantly in morphology and are less accurately classified to species when methods developed by Murray (1982) are utilized. The discrepancies between Murray's (1982) results and the results of this study are likely due, at least in part, to the general phenomenon of variation between populations in different localities. In the case of sibling species, variability in morphological characters may be nearly as great within species as between species when individuals are examined over a wide range of habitats.

Statistical techniques such as discriminant analysis can be powerful methods for distinguishing between morphologically similar species when other means are available initially to verify taxonomic status. Discriminant functions can be derived for particular habitats in cases where interhabitat variation in morphology is high, although other possible sources of variation (sex, season, parasitism) may still create difficulties in some circumstances. Ideally, specific techniques should be developed for specific applications. Discriminant analyses performed for certain local populations are not suitable for species as a whole, nor are analyses for species as a whole likely to be useful for specific local populations. Discriminant functions are potentially important tools for discriminating between specimens of *Littorina plena* and *L. scutulata* and other sibling species of gastropods but they should be used with caution and frequent re-evaluation.

ACKNOWLEDGMENTS

I appreciate the critical reviews provided by Drs. Richard Cowen, Cadet Hand, and David W. Phillips. I also thank

Edwin Mastro, Gregory Ruiz, and Jonathan Geller for their valuable comments, and Marian Marks and Laura Batie for assistance in preparing figures. This study is a contribution of the Center for Ecological Education and Research.

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